

Species Richness of Costa Rican Cenocoeliini (Hymenoptera: Braconidae): a Latitudinal and Altitudinal Search for Anomalous Diversity

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Abstract.—Latitudinal patterns of species diversity of New World Braconidae have been scarcely surveyed to date. Such patterns may be of biogeographical and ecological interest because some literature data suggest that some braconid subfamilies do not show an increase in species diversity towards the equator despite an increase of potential host species (i.e., "anomalous diversity"). In the present study, species diversity of a "presumptive" anomalous diverse braconid taxa, Cenocoeliini, was surveyed in Costa Rica. The results were compared with published distribution data of North American Cenocoeliini. Also, species richness and abundance of Cenocoeliini from sea-level to 3400 m altitude in Costa Rica were analyzed to compare latitudinal and altitudinal gradients in species diversity. Costa Rican Cenocoeliini were five times more speciose than those in Canada and USA combined. The increase in estimated species richness per unit area towards the equator of North American Cenocoeliini was similar to that of their most common hosts, Cerambycidae and Scolytidae, but exceeded that of the potential hosts in Costa Rica. Diversification in Costa Rican Cenocoeliini was partly influenced by adaptation to different host families and host substrates. Most species and individuals of Cenocoeliini were found at low altitudes (<500 m) in Costa Rica. Cenocoeliini were not encountered above 1600 m in Costa Rica, this being in contrast to their most likely hosts, Cerambycidae and Scolytidae, which also occurred at high altitudes. Larger-sized Costa Rican Cenocoeliini were often brightly colored suggesting an aposematic function towards visually-oriented predators. New World Cenocoeliini appeared to be tropical lowland-centered and this is expected to be rather an effect of temperature requirements than an effect of host-limitation.

Anomalous diversity is defined as a pattern in species richness "counter to the prevalent trend of increasing species number in a taxon with decreasing latitude" (Rathcke and Price 1976). Owen and Owen (1974) were the first investigators to show anomalous diversity for parasitic Hymenoptera of the family Ichneumonidae, despite an increase of numbers of potential host species towards the equator. Janzen and Pond (1975) found a similar pattern in species richness for parasitic Hymenoptera; they were less or equally speciose in Costa Rica compared to those occurring in a meadow in England. Several investigators noted that sweep-sampling studies of parasitic Hymenoptera in

the tropics may provide biased results for large-sized parasitoids (>3 mm) in areas where small-sized parasitoids may be abundant (Hespenheide 1979; Morrisson *et al.* 1979). More recently, results of Malaise trap sampling revealed that some subfamilies of Ichneumonidae displayed anomalous diversity (Gauld 1986, 1987, 1995b). Several theories to explain latitudinal patterns in species diversity of parasitic Hymenoptera have been formulated: resource fragmentation (Janzen and Pond 1975; Janzen 1981), predation on hosts (Rathcke and Price 1976), predation on parasitoids (Gauld 1987), and the "nasty" host hypothesis (Gauld *et al.* 1992; Gauld and Gaston 1994). According to these the-

ories, different ecological groups of parasitic Hymenoptera are expected to show different patterns in latitudinal species diversity (Hawkins 1994).

To date, anomalous diversity has not been fully analyzed for New World Braconidae. Quicke and Kruft (1995) found some subfamilies of Braconidae (e.g., Alysiinae, Aphidiinae, Cheloniinae) to be less speciose from northern (zone 3, 4) towards southern (zone 5) latitudes in the USA. This suggests anomalous diversity, however, these analyses did not include neotropical regions. Species richness of another group, Cenocoeliinae (i.e., Cenocoeliini), increased from northern to southern temperate regions, but did not increase from middle to lower latitudes in the USA (Quicke and Kruft 1995). Also, species richness of Cenocoeliini in southern temperate regions was equal to that of northern and central Mexico combined and to that of southern Mexico (data from Saffer 1982). To date, not more than two species of Cenocoeliini have been described from Costa Rica (Saffer 1977, 1982). Previous data, therefore, suggest a pattern of anomalous diversity in Cenocoeliini. The distribution of Central American Cenocoeliini, however, is less well documented than that of North America (Saffer 1982).

Cenocoeliini are diurnally active endoparasitic koinobionts of endophytic beetle larvae (van Achterberg 1994; Saffer 1982). In North America, Cenocoeliini were found to parasitize Cerambycidae (68% of recorded host species), Scolytidae (22%), and Buprestidae (Saffer 1982). Koinobionts are parasitoids which let their hosts continue to be mobile and defend themselves for a while after being parasitized. Koinobionts are expected to have more narrow host ranges than idiobionts (Askew and Shaw 1986; Gauld 1987; Hawkins 1994) and are often referred to as "specialist" parasitoids. Sheehan and Hawkins (1991), however, noted that comparisons of average host ranges between koinobionts and idiobionts have to be

evaluated carefully. Specialist parasitoids (i.e., koinobionts) associated to endophytic hosts may show, as predicted by the theories of resource fragmentation and predation on parasitoids, a (very) strong decrease in species richness from the temperate to tropical zones (Table 4.2, Hawkins 1994). At the other hand, these parasitoids may also show, as predicted by the theory of predation on hosts and that of the "nasty" hosts, a weak decrease to increase in species richness towards the equator. Thus, based on parasitizing behavior, contrasting predictions could be made for species richness of Costa Rican Cenocoeliini.

Species richness along altitudinal gradients may demonstrate patterns similar to those of latitudinal gradients (Brown 1988; Stevens 1992). Noyes (1989) noted that in general species diversity of parasitic Hymenoptera in an Indonesian rain forest was the highest at low altitudes (< 1000 m). Also the highest diversity of their hosts, e.g. Lepidoptera, was found at low altitudes (Holloway 1986). This suggests that, if patterns in latitudinal and altitudinal species richness are similar, anomalous diversity should not occur among parasitic Hymenoptera. Results of an altitudinal transect study in the Venezuelan Andes by Janzen *et al.* (1976) showed that species richness of parasitic Hymenoptera was as high at 200 m as at 1600 m, but that it was lower at high altitudes (3550 and 3600 m). The decline of species richness of parasitic Hymenoptera between 1600 and 3550 m was smaller than the decline of species richness of most other groups of insects such as other Hymenoptera (ants, bees, aculeate wasps) and other insect orders (e.g., Coleoptera and Lepidoptera). This suggests that some groups of parasitic Hymenoptera show anomalous diversity along altitudinal gradients. At a lower taxonomic level, tropical altitudinal species diversity of Ichneumonidea was found to differ among subfamilies (Gauld 1985; Gaston and Gauld 1993;

Gauld and Hanson, in press). Also, Ophioninae were found to have different patterns in altitudinal species diversities between tropical regions (Gauld and Hanson, in press).

As noted earlier, anomalous diversity has not been completely analyzed for New World Braconidae. Literature data suggest that the braconid tribe Cenocoeliini may show a decrease, or at least no increase, in species diversity towards the equator. Therefore, the aims of the present study were: 1) to determine whether species richness and α -index of diversity of the Cenocoeliini in temperate regions were higher than those in tropical regions, 2) to determine whether potential hosts of Cenocoeliini increased more in species richness towards the equator than their parasitoids, 3) to relate latitudinal species richness with altitudinal species richness, and 4) to determine whether abundance and species richness of Cenocoeliini were higher at intermediate and high than at low altitudes in Costa Rica. This research is the first in a series of analyses of different groups of Braconidae to be examined for species diversity in Costa Rica in relation to altitudes.

MATERIALS AND METHODS

The tribe Cenocoeliini is a monophyletic group in the Helconinae (Shaw 1995), although several authors placed the Cenocoeliini as the main tribe in a separate subfamily, Cenocoeliinae (van Achterberg 1984, 1993; Shaw and Huddleston 1991; Wharton 1993). Before the generic revision by van Achterberg (1994), most Cenocoeliini species were considered to be within the genus *Cenocoelius*.

Individuals of Cenocoeliini were collected with Malaise traps (85%) and the rest by hand netting in Costa Rica, mostly during the last 10 years. Hand collected specimens for this study were from H.A. Hespenheide (University of California, Los Angeles), F. Parker (University of Utah) and J.A. Ugalde (INBio, Instituto

Nacional de Biodiversidad, Costa Rica). Malaise traps were located in different habitat types and at different altitudes throughout Costa Rica as described by Gauld (1991, 1995a). Our analyses included ca 70 Malaise trap-years of samplings at ca 60 different sites. Therefore, sample coverage was expected to be reasonably representative for the Costa Rican fauna. From these samples, Braconidae were sorted and sent to the University of Wyoming for identification. Cenocoeliini were sorted and individuals were determined to morphospecies using the following set of characters: hindwing venation (relative length vein $1M+CU$ to $1M$, and $1M$ to $1r-m$); color patterns of head, mesosoma, metasoma, legs, ovipositor sheaths and antennae; body size; ovipositor length relative to forewing length; number of flagellomeres; and shape of apical flagellomeres. Additional characters, like sculpture patterns on the propisternum, apex of the propodeum, and vertex, were included to distinguish among presumptive sibling species complexes. Data by Saffer (1982) were used to compare species richness of Braconidae in North America with that in Costa Rica. Sample coverage and sample intensity for Mexico was relatively low and less representative for the area than those of Canada, USA and Costa Rica.

Two formulae were used to estimate expected species richness of the faunae (S^e) based on the numbers of individuals per species in a sample:

$$1. S^e = S^2 / (S - S_1) \quad (S_1 = \text{total number of species with one individual})$$

$$2. S^e = S + ((S_1)^2 / 2S_2) \quad (S_2 = \text{total number of species with two individuals})$$

The first formula of expected species richness (S^e) is derived from the formula of sample coverage $(1 - (N_1/I))$: Fagen and Goldmann 1977). In this formula, I is the total number of behavior types observed and N_1 is the total behavior types ob-

served only once. I was substituted with S and N_1 with S_1 . S^{c1} was calculated as the inverse of the sample coverage multiplied by the number of observed species (S). The second formula of expected species richness (S^{c2}), is that of Chao 1 as described in Colwell and Coddington (1994). In addition to species richness, α -index of diversity of the logarithmic series was calculated because of its good discriminant ability and its low sensitivity to sample size (Magurran 1988). To estimate species richness per unit area the formula $S_a = x/a^{0.25}$ was used (S_a = number of species per unit area, x = number of observed species in country or region, a = area of country or region (10^3 km²); MacArthur and Wilson 1967, Gaston *et al.* 1996). We also estimated species richness per unit area for the most important temperate hosts of Cenocoeliini, the Cerambycidae (data from Monne and Giesbert 1994) and the Scolytidae (data from Wood 1982; Wood *et al.* 1991).

To examine the effect of altitude on species richness of Cenocoeliini, we defined 4 altitude classes: low (0–500 m), low intermediate (500–1500 m), high intermediate (1500–2500 m) and high (>2500 m) altitudes. These altitude classes reflect the distribution of different habitat types as described by Gauld (1995a). We assumed that there was a linear relationship between sample effort (i.e., Malaise trap-months) and number of individuals caught in Malaise traps. Because seasonal variation in abundance of neotropical insects occurs (Owen and Chanter 1970; Wolda 1988, 1989; Wolda and Wong 1988), only Malaise traps which operated three or more consecutive months were included in the analysis, and abundances of Cenocoeliini were summed for several year-round Malaise trap samples. We estimated expected numbers of Cenocoeliini per altitude class by multiplying the total number of observed Cenocoeliini with the proportion of number of Malaise trap-months of a particular altitude class to the total

Table 1. Numbers of individuals (N), species richness (S), two estimates of expected species richness (S^{c1} , S^{c2} ; see materials and methods), α -index of diversity, numbers of localities (loc) and averaged local species richness (S_{loc}) of Cenocoeliini from Canada and USA combined, Mexico and Costa Rica.

	Canada + USA	Mexico	Costa Rica
N	1108	51	301
S	11	13	57
S^{c1}	11	24	96
S^{c2}	11	22	123
α -index	1.665	5.291	20.822
loc	233	13	48
S_{loc}	1.1 ± 0.3	1.5 ± 1.0	2.8 ± 4.4
(range)	1–3	1–4	1–25

number of Malaise trap-months. We tested whether observed and expected numbers were equal between low (<500 m) and higher altitude classes combined using a chi-square test (Sokal and Rohlf 1981).

RESULTS

In total, 290 individuals of Cenocoeliini were found from 80,000 to 90,000 Braconidae sampled in Costa Rica. The individuals of Cenocoeliini were divided into 55 morphospecies. The two described Costa Rican Cenocoeliini species by Saffer (1977, 1982) did not match our individuals and were added to our morphospecies resulting in a total of 57 species and 301 individuals (Table 1). From this set of 57 species, 44 species belonged to *Capitonius*, and 7 species to *Cenocoelius*. Of the remaining species, 4 species may belong to *Capitonius* but are rather distinctive and 2 species belong to a new genus of Cenocoeliini. The species varied in size from 3 to 12 mm. The ovipositors were relatively long, 0.7 to 1.7 times the forewing length. About half of the individuals and species were relatively large, mostly >5 mm, and bright yellow-orange to red-orange and often partly black in color, with partly to completely darkened wings. Most other individuals were relatively small, <7 mm, and blackish, brownish or black and dull red

Table 2. Estimated species richness per unit area (S_e) of parasitoids (Cenocoeliini) and their most common temperate hosts (Cerambycidae and Scolytidae) for different geographical regions of North and Central America, using $S_e = x/a^{0.25}$ as a standard species-area relationship (see text). Between parentheses are the relative richnesses when the estimated species richness of Canada was set at 1.0.

Geographical region	Area (10^3 km^2)	Cenocoeliini S_e	Cerambycidae S_e	Scolytidae S_e
Canada (+Alaska)	11,496	0.39 (1.0)	29.4 (1.0)	17.3 (1.0)
USA (-Alaska)	7,828	1.17 (3.0)	85.8 (2.9)	50.3 (2.9)
Mexico	1,969	1.95 (5.0)	201.2 (6.8)	90.8 (5.2)
Costa Rica	51	21.36 (54.8)	260.1 (8.8)	155.3 (9.0)

to reddish brown in color with clear wings, sometimes with brownish spots on the forewings.

Highest species richness was found in Costa Rica and lowest species richness in Canada and USA combined (Table 1). Both estimators of expected species richness (S_e^1 and S_e^2) predicted that in Mexico and Costa Rica about half of the total number of species have been caught to date. More species were found in 2 Costa Rican Malaise trap sites (Heredia Province, Biological Station of OTS La Selva, and Puntarenas Province, 24 km west of Piedras Blancas) than in all trap sites of Mexico or Canada and USA combined. The highest diversity (α -index) was found for Costa Rican Cenocoeliini, the lowest for those of Canada and USA combined.

The increase of estimated species richness per unit area for North American Cenocoeliini was similar to that of their most common hosts (Table 2). On average, 3 times more species per unit area occurred in the USA than in Canada and about twice as many species per unit area occurred in Mexico compared to the USA. In contrast, Costa Rican Cenocoeliini were 11 times more speciose per unit area than in Mexico, meanwhile the potential hosts increased only about 1.5 times in species richness per unit area for the same areas.

Cenocoeliini were most speciose at low altitudes in Costa Rica (Table 3). Specimens were not encountered above 1600 m and Cenocoeliini were, significantly, more

abundant at low (<500 m) than at higher (>500 m) altitudes.

DISCUSSION

The increase of species richness of Cenocoeliini from Canada to Mexico was equal to that of their common hosts and exceeded that of their potential hosts in Costa Rica. Hence, anomalous diversity could not be shown for New World Cenocoeliini. This is in contrast to the prediction by resource fragmentation (Janzen and Pond 1975; Janzen 1981) suggesting that tropical host trees and their associated host beetles are too widely distributed to be exploited by koinobiont parasitoids. To illustrate this fragmentation, one ha of tropical lowland rain forest in Costa Rica contained 3 to 4 times more tree species than one ha of the most diverse North American forests (Hartshorn 1983; Whittaker 1965). Also a 50 ha moderate diverse lowland rain forest in Panama contained an equal number of tree species as the whole of western North America, north of Mexico (Condit *et al.* 1996; Little 1980). Janzen's (1981) caveat to resource fragmentation was that tropical koinobiont parasitoids had developed a broader host range compared to temperate koinobionts, or that they had become very efficient in looking for sparsely distributed hosts. In the present study, this could not be analyzed for neotropical Cenocoeliini, partly due to the lack of host records. North American Cenocoeliini, on average,

Table 3. Total species richness (S), number of Malaise trap-months (# tm), observed (N_{obs}) and expected (N_{exp}) numbers of individuals of Cenocoeliini per altitude class in Costa Rica. Only Malaise traps which operated more than three consecutive months were included in the analysis. It was tested if the observed and expected numbers of Cenocoeliini were equal at low altitudes (<500 m) and at higher altitude classes combined using chi-square test.

Altitude class	S	# tm	N_{obs}	N_{exp}	χ^2 (df = 1)
≤500 m	48	546	219	155	78.27
500–1500 m	16	71	8	20	(P < 0.001)
1500–2500 m	5	138	7	39	
>2500 m	0	72	0	20	
Totals	57*	827	234	234	

* Twelve species occurred at the two lowest altitude classes; one species occurred from 0–1600 m. Individuals were not found above 1600 m altitude.

parasitize one to 4 different host species (Saffer 1982). This “narrow” host ranges would classify the North American Cenocoeliini as specialists, however, we have to be careful to generalize, because these host records were not complete (Shaw 1994).

Results of the present study showed that the increase in species richness per unit area of Cenocoeliini from Mexico to Costa Rica was 6 times larger than that of their potential hosts (Table 2). This suggests that Costa Rican Cenocoeliini parasitize a larger proportion of the Cerambycidae and Scolytidae, than those in North America. At the other hand, some Costa Rican Cenocoeliini may have adapted to other beetle families of beetles with a different biology. The only known host record from Cenocoeliini in Costa Rica was that of a species attacking seed-boring beetle larvae of the family Curculionidae (Saffer 1977). Long-term research on seed-boring beetles in Costa Rican dry forest (Janzen 1980), however, did not reveal additional observations of Cenocoeliini on seed-boring beetles (Janzen, pers. comm.). Five percent of our surveyed specimens of Cenocoeliini from Costa Rica were collected from treefalls by hand (Hespenheide, unpublished data) and other micro-habitats not were indicated on the collecting labels. We expect, therefore, that wood-

and bark-boring insects are the most likely host for Costa Rican Cenocoeliini.

In the present study, we found that fewer species of Cenocoeliini occur at intermediate than at low altitudes (Table 3). This is comparable to the reduction in species richness towards the equator (Table 1). But the decline in species richness of Cenocoeliini with altitude in Costa Rica was higher than expected. As shown in the present study, Cenocoeliini were not encountered at 2000 m in Costa Rica. At latitudes in temperate North America with a similar mean yearly temperature, however, 5 to 8 species of Cenocoeliini occurred (Quicke and Kruff 1995). In Costa Rica, seasonal changes in temperature are usually smaller than diurnally fluctuation in temperature (Gauld 1995a). In temperate regions this is often reversed. These differences in temperature regimes may affect species richness of New World Cenocoeliini.

Individuals of Cenocoeliini were not encountered at altitudes higher than 1600 m, even though a total of 150 Malaise trap-months located at 10 different sites were surveyed. This was an unexpected observation as potential hosts of Cenocoeliini have been observed at high altitudes. Cerambycidae are most abundant at low altitudes in Costa Rica but occur also at high altitudes up to timberline (3200–3400 m;

Lezama, pers. comm.). Scolytidae are known to be regularly encountered at high altitudes in Costa Rica (Wood *et al.* 1991). It is unlikely, however, that alternative hosts for Cenocoeliini, like larvae of seed-boring beetles do occur at high altitudes. Legume trees, of which the fruits are among the most frequently attacked by seed-boring beetles (Janzen 1980), are scarce at intermediate and absent at high altitudes (Holdridge *et al.* 1971). Also, Gaston and Gauld (1993) noted that Pimplinae (Icneumonidae) were more abundant at high altitudes than at low altitudes. In case species of Cenocoeliini would have been present at high altitudes in Costa Rica, they likely would have been collected in the Malaise traps. This suggests that host presence does not explain absence of Cenocoeliini at high altitudes in Costa Rica.

In the present study, it could not be determined if Cenocoeliini were scarce in Costa Rica or that it is difficult to sample them by using Malaise traps. On average, one individual of Cenocoeliini was caught per 3 to 4 Malaise trap-months. Trap efficiency for Cenocoeliini was twice as high at low altitude rain forests than at low middle altitude rain forest or low altitude dry forest. Also Cenocoeliini were most frequently caught during the dry season (Feb.–May; unpublished data). But even in the optimal habitat type and season, Cenocoeliini was never found to be abundant suggesting that they occur in low population densities.

Another remarkable result was that 77% of the Mexican and 60% of the Costa Rican species of Cenocoeliini were represented by one or 2 individuals. Estimated species richness of Mexican Cenocoeliini may have been underestimated as sample coverage by the Malaise traps in Mexico was low compared to those in Costa Rica and the USA and Canada combined.

Analyses of geographical distribution of Costa Rican Cenocoeliini could not be justified due to low numbers of individuals

in Malaise traps. The observed 24 Cenocoeliini species in the Pacific lowland rain forest around Golfo Dulce in Puntarenas Province shared 9 species with the 25 Cenocoeliini species in the Atlantic lowland rain forest of La Selva in Heredia Province. This species distribution of Cenocoeliini may suggest that many Costa Rican Cenocoeliini have a restricted geographical distribution according to Rapoport's Rule (Stevens 1989, 1992). It may also be a sample artifact due to the low number of individuals.

In the present study it was found that half of the Cenocoeliini and especially those larger than 5 mm were bright orange and black colored, often with partly or completely darkened wings. Saffer (1982) described 2 similar bright colored Cenocoeliini from southern tropical Mexico, but no such colored species from temperate North America. Bright colors are common in tropical parasitoids (Quicke 1986a; Shaw 1995). Bright colors occur in several other neotropical braconid subfamilies such as Agathidinae and Braconinae and they are characteristic for larger sized (>5 mm) diurnally active Braconidae with long ovipositors, which likely parasitize concealed hosts (Shaw 1995). In general, bright colors are characteristic for lowland insects where it occurs in up to 25% of insects and do not occur at high altitudes in Costa Rica (Janzen 1973). Quicke (1986b) noted that in general bright colors have a warning function towards visually-oriented predators (i.e., aposematic coloration). Bright colored tropical parasitic wasps may mimic stinging aculeates and some larger sized parasitoids are capable of stinging by themselves (Quicke 1986b). Other authors hypothesized that parasitoids may mimic unpalatable hosts such as Chrysomelidae (Gauld, pers. comm.) or Symphyta (anon. rev., pers. comm.). Gauld and Gaston (1994), suggested that parasitoids with bright colors may be unpalatable for predators after sequestering "nasty" tasting

secondary plant chemicals from their hosts. If the latter is true and the "nasty" host hypothesis has validity for Cenocoeliini, bright colored Cenocoeliini may attack seed-eating or phloophagous beetle larvae, rather than wood-living Scolytidae or Cerambycidae. Quicke (1986a) found homeochromatic assemblages for some large sized Braconidae and their potential hosts (i.e., Cerambycidae). Hespeneheide (1996) showed that color patterns of Chrysomelidae may be substrate-related. More research is needed to elucidate the underlying defense mechanisms or other meaning of bright colors in large sized neotropical wood-boring braconid parasitoids.

The smaller sized Costa Rican Cenocoeliini from our survey were mostly less conspicuous colored than the larger sized ones. Many of these smaller sized Cenocoeliini may be ant-mimics, which is expected to occur frequently in neotropical Braconidae (Shaw 1995). This color pattern of presumably ant-mimics also occurred among North American Cenocoeliini (Saffer 1982). To date, possible behavioral and olfactorial cues involved in ant-mimicry of Braconidae have not been documented.

In conclusion, the results of the present study showed that the species diversity of the Cenocoeliini increases towards the equator. This is the normal pattern in latitudinal species richness (Fisher 1960; Pianka 1966; Stevens 1989; Wilson 1992). Thus, anomalous diversity was not observed for Cenocoeliini. The increase in species richness per unit area of Cenocoeliini from temperate North America to the Neotropics exceeded that of their potential hosts. In Costa Rica, species and individuals of Cenocoeliini were not found above 1600 m altitude, this in contrast to their potential hosts which also occur at high altitudes. This suggests that species richness in Cenocoeliini is not host limited. The Cenocoeliini apparently is a tropical lowland-centered group of which a limited

number of species have adapted to year-round cool conditions at lower montane rain forests and none to montane forests. Some other species have adapted to climatological conditions in temperate regions and evolved overwintering mechanisms (Saffer 1982).

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